Revision of the egg morphology of *Eulimnadia* (Crustacea, Branchiopoda, Spinicaudata)

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ABSTRACT
The egg morphology of *Eulimnadia* is presented on the basis of samples stored in the Muséum national d'Histoire naturelle, Paris, representing 11 species one of which unidentified. Study of all specimens revealed the presence of nine different egg types. Seven types could clearly be assigned to one species, six of which after eggs produced by the type specimens of the species. In addition, the identification of the specimens labelled "*E. colombica*" as *E. geayi* was confirmed, the identification of an *E. magdalensis* population initially identified as *E. compressa* was corrected, the species *E. chaperi* is considered as valid, and a new egg type representing a potential new species was described. Seven instances of contamination from five species were identified, demonstrating that small eggs can easily contaminate samples during collection handling. Advice on museum collection management, a synthesis of the knowledge on egg morphology and an identification key of described *Eulimnadia* eggs is presented in order to prepare a general revision of this genus based on the egg morphology, which provides informative specific characters.

KEY WORDS
Crustacea,
Branchiopoda,
Spinicaudata,
Limnadiidae,
Eulimnadia,
SEM,
egg morphology.

RÉSUMÉ

*Révision de la morphologie des œufs d'*Eulimnadia *(Crustacea, Branchiopoda, Spinicaudata).*

La morphologie des œufs d'*Eulimnadia* est présentée sur la base d'échantillons conservés au Muséum national d'Histoire naturelle, Paris, représentant 11 espèces dont une indéterminée. L'étude de tous les spécimens révèle la présence de neuf types différents d'œufs : sept peuvent être assignés à une espèce, dont six d'après les œufs produits par les spécimens types des espèces concernées. De plus, l'identification des spécimens étiquetés « *E. colombica* » comme étant *E. geayi* a été confirmée, l'identification d'une population de *E. magdalensis* initialement identifiée comme *E. compressa* a été corrigée, l'espèce *E. chaperi* est considérée comme valide et un nouveau type d'œuf représentant une potentielle nouvelle espèce a été décrit. Sept cas de contaminations provenant de cinq espèces ont été identifiées, ce qui démontre que les petits œufs peuvent facilement contaminer les échantillons durant les manutentions de la collection. Des conseils sur la gestion des collections, une synthèse des connaissances sur la morphologie des œufs et une clé d'identification des œufs d'*Eulimnadia* décrits sont présentés dans l'objectif de préparer une révision générale du genre basé sur la morphologie des œufs, le plus informatif des caractères spécifiques.

MOTS CLÉS
Crustacea,
Branchiopoda,
Spinicaudata,
Limnadiidae,
Eulimnadia,
MEB,
morphologie des œufs.

INTRODUCTION

Spinicaudatan systematics is traditionally based on morphological characters. However a majority of these characters seem to be variable. Indeed, in *Cyzicus tetracerus* (Krynicki, 1830), as well as in *Eulimnadia magdalensis* Roessler, 1990, the elevation of breeding temperature induced a reduction of the final size and number of growth lines reached at sexual maturity (Massal 1954; Roessler 1990, 1995). More generally the number of growth lines depends on the number of moults and, logically, on the age of the animal (Massal 1953 for *Cyzicus* Audouin, 1837 and Vidrine *et al.* 1987 for *Eulimnadia* Packard, 1874) and could therefore not be directly used systematically. Additionally, the intraspecific variability of characters, especially of the head shape, has sometimes been used to generate artificial species, as for *Imnadia yeyetta* Hertzog, 1935 (Straskraba 1965) or *Eulimnadia diversa* Mattox, 1937 (Belk 1989). These different morphological variations generated species level confusion, principally because in the past, the majority of species were described using these characters. Spinicaudatan systematics needs to be revised and redefined, through the addition of specific discriminatory characters that are constant at the population level. This is especially needed for the genus *Eulimnadia*, the most diverse spinicaudatan genus, and recently confirmed as a valid evolutionary entity (Hoeh *et al.* 2006; Schwentner *et al.* 2009). In this genus, except for some specific characters (as in the extreme reduction of telson spines in *Eulimnadia antillarum* (Baird, 1852) few adult morphological characters are useful at the specific level. The relative size of the caudal furca first spinule, or the male rostrum shape, were recently defined as useful for some taxa (Pereira & Garcia 2001), but the combination of these morphological characters is insufficient for species diagnosis except in limited, well-studied, areas.

Fortunately, as in other Limnadiidae and several groups of Branchiopoda, the ornamentation of the eggs are sometimes described in traditional systematic works (see Table 2). In *Eulimnadia*, the first egg morphology description was made by Guérin (1837) (described as *Limnadia mauritiana*). The egg shape was sometimes discussed in a taxonomic perspective (see Ihering 1895) and sometimes described and figured (Sars 1896 1900, 1902; Daday de Deés 1926). However, since 1989, the egg morphology has been used as a good systematic

TABLE 1. — Different egg morphologies in *Eulimnadia* Packard, 1874 present in the MNHN collection. **+**, eggs from cluster under the shell; °, probably contaminated eggs; **?**, uncertain assignation. Details given in the text.

Egg types	Figures	MNHN collection sample	Species identification
Spherical with spiral ornamentation	1A-D	MNHN-Bp316, 317, 321°	*E. acutirostris* Daday de Deés, 1926 (type specimen)
Spherical with rectangular depressions	1E-I	MNHN-Bp318	*E. aethiopica* Daday de Deés, 1926 (type specimen)
Pentagonal with large and round ridges	2A-D	MNHN-Bp319+	*E. alluaudi* Daday de Deés, 1926 (type specimen)
Cylindrical with equal border size	–	MNHN-Bp321	*E. antillarum* (Baird, 1852)?
Spherical with large depression ornamented by holes	2E-H	MNHN-Bp319°, 320°, 325-329+	*E. chaperi* (Simon, 1886) (type specimen)
Pentagonal with narrow ridges	3A-C	MNHN-Bp321°, 323, 324, 330, 331	*E. geayi* Daday de Deés, 1926 (type specimen)
Twisted	3D-I; 4A-C	MNHN-Bp320°, 328°, 332-334+, 467°	*E. mauritiana* (Guérin, 1837) (type specimen)
Spherical with large depression without ornamentation	4D, E	MNHN-Bp467°, 325+, 328+	*E. magdalensis* Roessler, 1990
Oblong with long depression	4F-I	MNHN-Bp667+	*Eulimnadia* sp.

character, more efficiently explored using scanning electron microscopy (SEM) on American species (Belk 1989; Martin 1989; Martin & Belk 1989; Roessler 1989, 1990; Brendonck *et al.*, 1990; Cesar 1990; Smith 1992; Smith & Wier 1999; Pereira & Garcia 2001; Smith & Little 2003). Some works performed outside of the Americas strongly support the global use of this character (Thiéry 1996; Timms & McLay 2005; Shen & Huang 2008).

Before 1989, some egg morphological descriptions were imprecise or mistakes were made due to technical limitations. However, the systematic clarification of *Eulimnadia* implies that eggs from all species should be described or re-described using SEM and standardized terminology. In consequence, I present *Eulimnadia* egg descriptions from material stored in the Muséum national d'Histoire naturelle, Paris (MNHN), as a preliminary to revising this genus.

MATERIAL AND METHODS

All specimens come from the MNHN collection and are registered with a number following the letters Bp (MNHN-Bp316 to MNHN-Bp334, MNHN-Bp467, MNHN-Bp468 and MNHN-Bp667) representing *Eulimnadia* collected in Cambodia, Gabon, India, Madagascar, Mauritius Island, Mexico, Santo Domingo, Venezuela and West Africa. Eggs from each sample were isolated and dehydrated following a critical point treatment procedure using CO_2. This step was necessary for the majority of old specimens as opposed to recent material, which can be directly dried with little damage to the egg structure.

Individual eggs were removed from under the parent's carapace. If eggs are not available in animals they are collected in the bottom of the bottle but in this case the assignment is problematic (see Discussion).

RESULTS

Ten species determined by Daday de Deés and one undetermined are stored in the MNHN crustacean collection. Study of all specimens is summarized in Table 1 and revealed the presence of nine different egg types. Seven egg types could clearly be assigned to a species, including eggs from six type specimens. In addition, it is confirmed that the specimens labelled "*E. colombica*" (handwritten name, not nomenclaturally available) correspond to *E. geayi* Daday de Deés, 1926, the identification of an *E. magdalensis* population initially identified as *E. compressa* (Baird, 1860) was corrected, the species *E. chaperi* (Simon, 1886) is considered as valid, and a new egg type representing a potential new species was discovered. However, a type of cylindrical eggs were more difficult to assign, due to the possibility of contamination. Indeed seven instances of contamination among five species were identified, demonstrating that small eggs can easily contaminate samples during collection handling.

For each species stored in the MNHN, detailed egg morphology information is presented.

Eulimnadia acutirostris Daday de Deés, 1926 (Fig. 1A-D)

Eulimnadia acutirostris Daday de Deés, 1926: 513, fig. 126.

Limnadia acutirostris – Brtek 1997: 56.

TYPE LOCALITY. — A temporary pool in Simbidissi and Hogui in the middle part of Niger Basin in French West Africa during the collecting period (Daday de Deés 1926) and now in Niger or in Mali.

MATERIAL EXAMINED. — Middle part of the Niger Basin, Hogui, temporary pool, 8.VI.1909, D. R. Chudeau, 5 eggs from the bottom of the bottles (MNHN-Bp316, 317).

RANGE. — The present knowledge of egg morphology leads us to considerer this species as known only from type locality.

EGG MORPHOLOGY

Spherical egg covered by spiral ridges. The bottom of the furrows are narrow and the ridges separating them are large and round (Fig. 1D). The ridges are complexly fused where they intersect (Fig. 1A). Average egg diameter is 139.5 µm (n = 2, SD = 2.12 µm).

REMARKS

The eggs, described from the type specimens only, and coming from the bottle bottom, match the original description, "Ova membrana spiraliter plicata tecta" of Daday de Deés (1926). Long furrows are also present in *Imnadia yeyetta* oval eggs (Thiéry & Gasc 1991). However the fusion area of the furrows in *Eulimnadia acutirostris* is complex because there are several parallel furrows while in *Imnadia yeyetta* the furrow is unique and forms a spiral with a simple end at the apex. In the studied eggs, the surface is partially covered by micro-organisms and mud.

Eulimnadia aethiopica Daday de Deés, 1926 (Fig. 1E-I)

Eulimnadia aethiopica Daday de Deés, 1926: 546, fig. 137.

Limnadia aethiopica – Brtek 1997: 56.

TYPE LOCALITY. — Indicated by Daday de Deés (1926) as coming from Sudan. However, the collector designated the Kousseri area (Kousri in Daday de Deés and on the sample label), a town of the north-east of Cameroon, very near the Chad border, near N'djamena. It is impossible to say if the collection came from present Chad or Cameroon.

MATERIAL EXAMINED. — The Kousseri Area, Chari Tchad Mission ("Chari Soudanai, Kousri"), VIII.1903, J. Decorse, >10 eggs (MNHN-Bp318).

RANGE. — Based on egg morphology, this species appears restricted to the type locality for the present, however see Remarks below.

EGG MORPHOLOGY

Spherical egg with approximately rectangular depressions randomly distributed at the egg surface. The bottom of the depressions is very narrow and linear, and the ridges separating them are narrow and relatively sharp (Fig. 1H, I). In detail, the egg surface is relatively smooth (Fig. 1I). Average egg diameter is 178.1 µm (n = 8, SD = 5.4 µm).

REMARKS

The original drawing and description of the egg, indicating "Ova membrana tuberculata, tuberculis utcunque coniformibus armata tecta", is compatible with the eggs studied here. This species has a spherical rough egg which is widespread in the world and has already been reported from Sudan

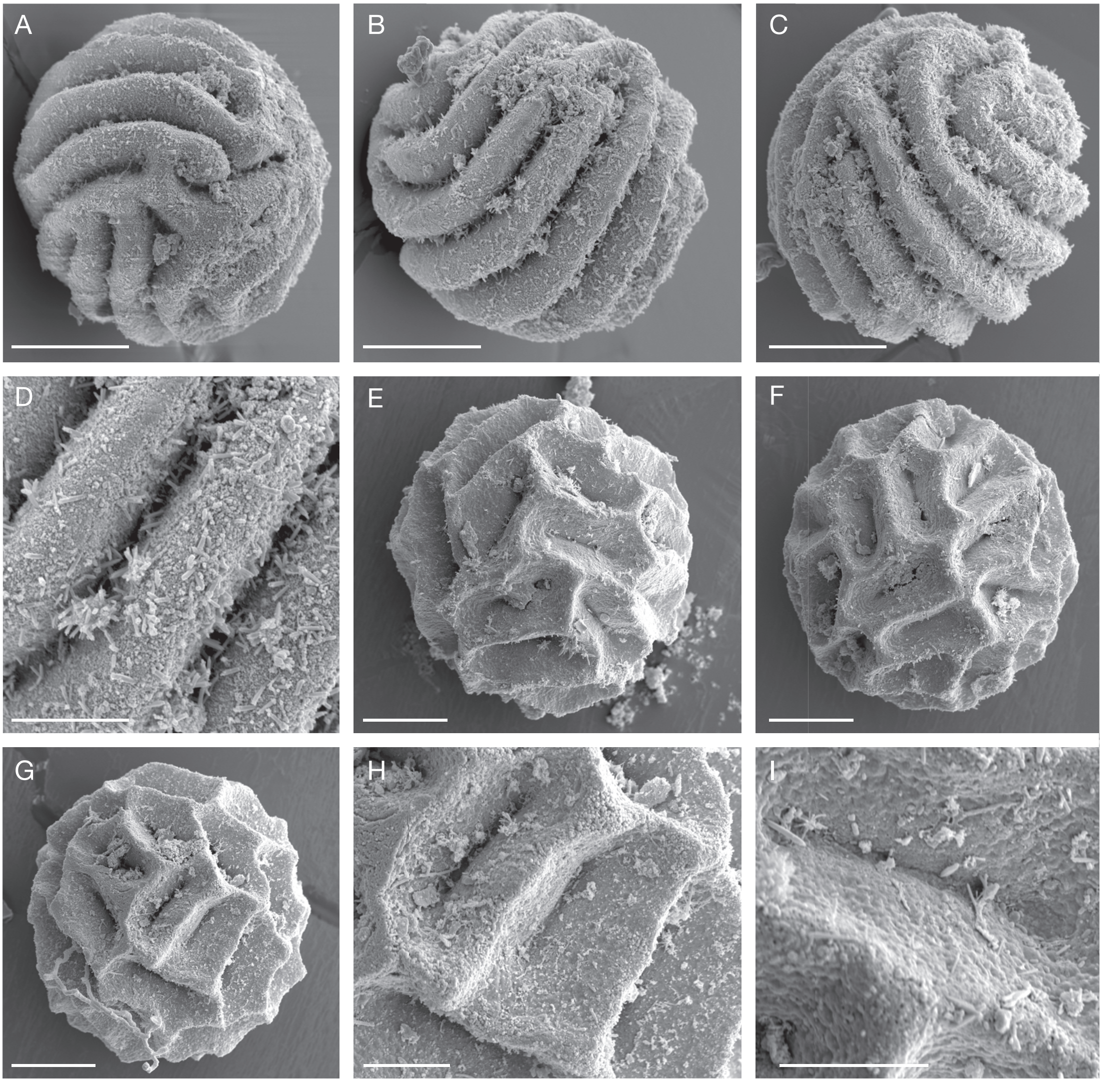

Fig. 1. — Eggs morphology: **A**-**D**, *Eulimnadia acutirostris* Daday de Deés, 1926, eggs from the type specimen; **E**-**I**, *Eulimnadia aethiopica* Daday de Deés, 1926, eggs from the type specimen. Scale bars: A-C, E-G, 50 µm; D, H, I, 20 µm.

(*E. africana* (Brauer 1877)), south of Africa (reported as *E. africana* by Barnard 1929), Arabia (*E. margaretae* by Thiéry 1996), South America (*E. brasiliensis* Sars, 1902 or *E. ovilunata* Martin & Belk, 1989 by Martin 1989; Martin & Belk, 1989 and Pereira & Garcia 2001) and also China (*E.* sp. Shen & Huang 2008). A careful examination of this type of egg using SEM could provide strong argument to clearly define each species according to the date of description. Indeed, at present eggs of *E. africana*, the first species described with this type of egg morphology, are not yet described using SEM.

Eulimnadia alluaudi Daday de Deés, 1926
(Fig. 2A-D)

Eulimnadia alluaudi Daday de Deés, 1926: 567, fig. 144.

Limnadia alluaudi – Brtek 1997: 56.

Type locality. — Daday de Deés (1926) reported two localities for this species. The first locality is considered as the type locality, and that sample was studied here (south of Madagascar in Bekitro commune). The other locality is from Topani, between Sekuma in Kalahari state, collected by L. Schultze the 4 November 1897 (Bostwana). It is possible that each population represents a separate species.

Material examined. — **Madagascar.** Manambahy, Bekitro, 1901, Ch. Alluaud, > 100 eggs (MNHN-Bp319)

Range. — The present knowledge of egg morphology suggests this species is restricted to the type locality as defined above, in the south of Madagascar. The other population, in southern Africa, needs to be investigated.

Egg morphology

The eggs, collected in the bottom of the bottle and in position below the carapace, have a more or less cylindrical structure with a wider, very inflated side creating a pentagonal shape, though in some orientations the eggs seem to be spherical (compare eggs in Fig. 2A and Fig. 2B with Fig. 2C). The furrows covering the main cylindrical part of the egg are parallel, but on the inflated side the furrows are randomly distributed. The furrow bottoms are narrow, while the ridges are large and round. In detail, the surface bears very small pores (Fig. 2D). Average egg height is 175 µm (n = 3, SD = 7.9 µm).

Remarks

Following Daday de Deés (1926), the egg of this species was firstly described as "Ova membrana tuberculata tecta". The drawings suggest that the egg is spherical and ornamented by numerous peaks, which is not exactly compatible with the egg described here. However, the examined eggs were in natural position and clustered, thus excluding contaminations. Pentagonal eggs are also known in *E. geayi* (see Martin 1989; Pereira & Garcia 2001 and this study) though in *E. alluaudi* the inflated side seems to be more inflated than in *E. geayi* thus presenting an outline more spherical than cylindrical. In addition the two species are distinct because in *E. geayi* the bottom of furrows seems to be larger and the ridges sharper, and not rounded as in *E. alluaudi*. Among typical *E. alluaudi* eggs, I found in the bottom of the bottle, one spherical egg identical to those described for *E. chaperi*; I interpreted it as a contaminant.

Eulimnadia antillarum (Baird, 1852)

Limnadia antillarum Baird, 1852: 30, tab. 23, fig. 1. — Packard 1874: 314. — Simon 1886: 456. — Lilljeborg 1889: 424. — Brtek 1997: 56.

Eulimnadia antillarum – Ihering 1895: 173. — Daday de Deés 1926: 517, fig. 127. — Martin 1989: 108, fig. 5A.

Type locality. — Island of Hispaniola.

Material examined. — **Mexico.** 2 eggs (MNHN-Bp320); 3 eggs (MNHN-Bp321). — Island of Hispaniola, female without eggs (MNHN-Bp322).

Range. — In addition to the type locality, this species was indicated in Mexico (Daday de Deés 1926) and in Brazil (Lilljeborg 1889). The latest citation is doubtful because the diagnostic caudal region is unknown in this population.

Egg morphology

Four types of egg morphologies are represented: one (from MNHN-Bp320) is similar to those of *E. mauritiana*, one (from MNHN-Bp321) is similar to those of *E. acutirostris*, one (from MNHN-Bp 320) is similar to those of *E. chaperi*, and one (from MNHN-Bp321) is similar to those of *E. geayi*. A cylindrical egg with equal border size was also found in MNHN-Bp321 but unfortunately destroyed during the critical point operation and was observed only under stereomicroscope.

Remark

As cylindrical with equal border size eggs are not present in other samples in MNHN, this type of eggs could be not a contamination, and gives impetitus for finding current populations of *E. antillarum* in Mexico.

Eulimnadia chaperi (Simon, 1886)
(Fig. 2E-I)

Limnadia chaperi Simon, 1886: 455, tab. 7, fig. 3.

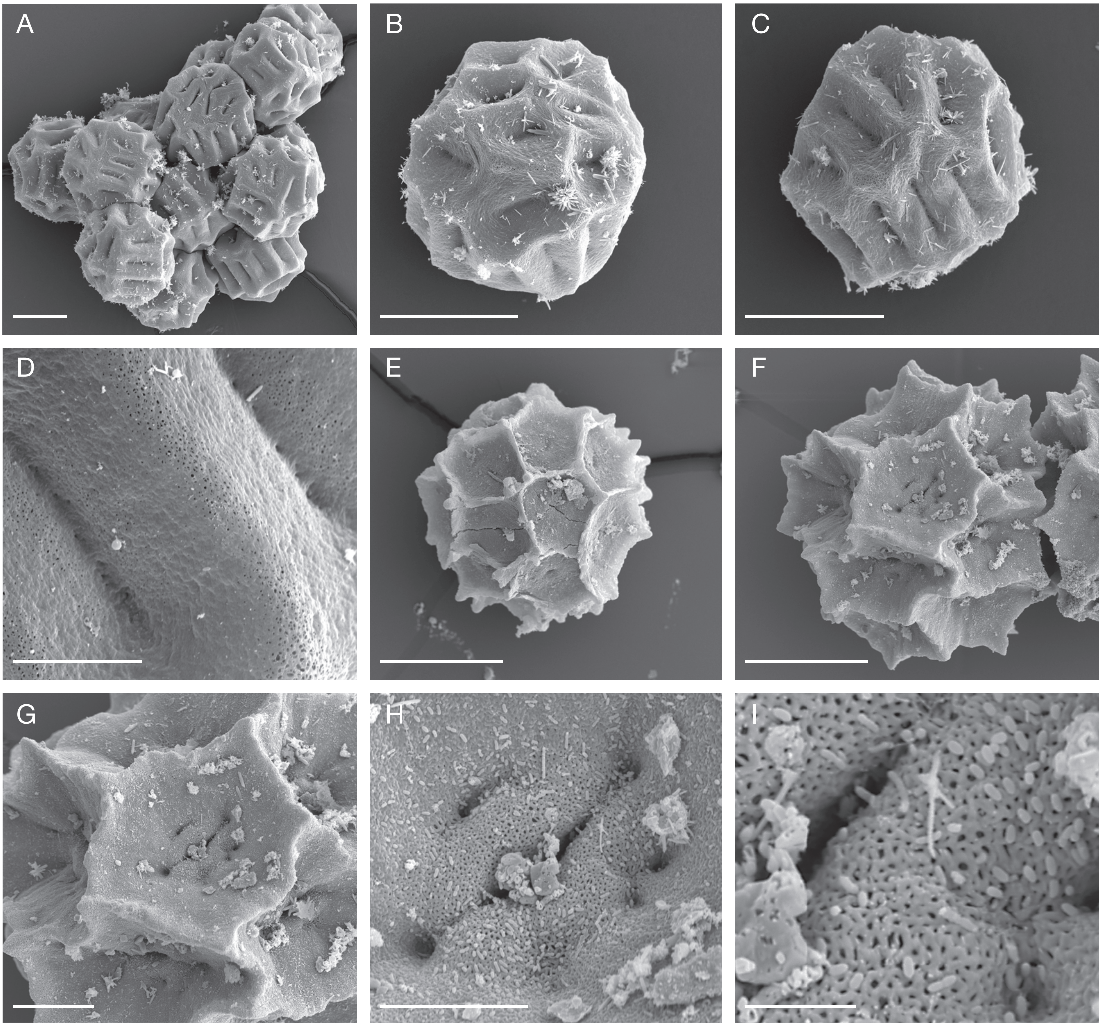

Fig. 2. — Eggs morphology: **A**-**D**, *Eulimnadia alluaudi* Daday de Deés, 1926, eggs from the type specimen; **E**-**I**, *Eulimnadia chaperi* (Simon, 1886), eggs from the type specimen; **E**, immature egg; **F**-**I**, mature eggs. Scale bars: A-C, E, F, 100 µm; D, G, H, 20 µm; I, 5 µm.

Eulimnadia compressa – Daday de Deés 1926: 558, fig. 140.

Type locality. — Vajra Karur near Bellary in Karnataka state, India.

Material examined. — **India.** "Wagra Karour" (Vajra Karur) near Bellary, Chaper, >100 eggs (MNHN-Bp326); >100 eggs (MNHN-Bp327); >100 eggs (MNHN-Bp329).

Range. — This species is known from the type locality only.

Egg morphology

Spherical with approximately pentagonal, broad, flat depressions separated by high ridges. Ridge interconnections with spiniform projections. The depression bottoms are ornamented by more or less defined holes: one at the centre and one in each angle of the pentagon. In some cases, furrows joined holes. At high magnification the surface of the egg is perforated by very small pores (Fig. 2H, I). The immature eggs have a similar shape but only the central depression is partially visible (compare

Figure 2E with Figure 2F). Average mature egg diameter is 218,4 µm (n = 9, SD = 10.9 µm).

Remarks

Simon (1886) described this species using these specimens stored in MNHN. Daday de Deés (1926) later considered this species a synonym of *E. compressa*. However the egg morphology of the *E. compressa* type specimen are unknown and it seems that the specimen identified by Daday de Deés as *E. compressa* has a different egg morphology. Indeed, the general description of the egg "Ova membrana reticulata, reticulis magnis, in angulis aculeate secta" and drawings are compatible with the two populations stored in the MNHN collection. However, using SEM, the depression bottoms differ (compare Figure 2H and Figure 3F). The eggs of *E. magdalensis* (Rossler 1990; Pereira & Garcia 2001 and specimens from Cambodia) have a similar general shape. However the depression bottom is not ornamented with holes or furrows, as is in these specimens. Following Sars (1896, 1900) and Daday de Deés (1926), *E. dahli*, *E. garreti* and *E. similis*, respectively indicated from Australia, French Polynesia and India, also seem to have this egg morphology. However SEM is necessary to confirm the similarities, especially the occurrence of holes or furrows in the depression bottoms.

Eulimnadia compressa (Baird, 1860)

Estheria compressa Baird, 1860: 188, tab. 71, fig. 6.

Limnadia compressa – Simon 1886: 452. — Brtek 1997: 57.

Eulimnadia compressa – Daday de Deés 1926: 558, fig. 140.

Type locality. — Nagpur, in the state of Maharashtra, India.

Range. — This species is probably well distributed in India but without egg morphology indications from the type specimen we should consider all other citations as doubtful.

Remarks

Under this name Daday de Deés included two populations stored in MNHN but they have differing egg morphologies (compare Figure 2H and Figure 3F) and are determined in this paper as *E. chaperi* and *E. magdalensis*. No description of the *E. compressa* type specimen egg morphology is available, making it problematic to use this name without morphological analysis of the type specimens or without an extensive survey of *Eulimnadia* populations in the area of the type locality.

Eulimnadia geayi Daday de Deés, 1926 (Fig. 3A-C)

Eulimnadia geayi Daday de Deés, 1926: 553, fig. 139. — Martin 1989: 108, fig. 4D-F. — Pereira & Garcia 2001: 642, figs 2, 9B.

Limnadia geayi – Brtek 1997: 57.

Type locality. — Sarare, probably in Venezuela, is the first locality indicated in the descrition (Daday de Deés 1926) (see Remarks).

Material examined. — **Venezuela.** Guanaparo, Geay, 1899, > 10 eggs (MNHN-Bp330). — Plains between Apure and Guanaparo rivers, Geay, 1892, >10 eggs (MNHN-Bp331). — "Haut Sarare", Geay, >10 eggs (MNHN-Bp323, 324).

Range. — Various places in Venezuela (Daday de Deés 1926; Pereira & Garcia 2001). Localities in Mexico (Daday de Deés 1926) should be confirmed by genetic or egg morphology studies.

Egg morphology

Cylindrical eggs with one end wider and domed, giving a vaguely pentagonal shape. The narrow ridges are parallel along the length of the cylinder, separating large depressions, and are produced apically. However in the domed end, the furrows are randomly distributed, delimiting more or less hexagonal depressions. For one egg in good position for measurements, height is 171 µm and diameter is 145 to 182 µm.

Remarks

According to Daday de Deés (1926), MNHN-Bp330 and MNHN-Bp331 (Fig. 3C) were collected in Venezuela and MNHN-Bp323 and MNHN-Bp324 (under the unpublished name *E. colombica*) in Colombia. However "Sarare" indicated by Daday de Deés in Colombia is a homonym of the type locality which is

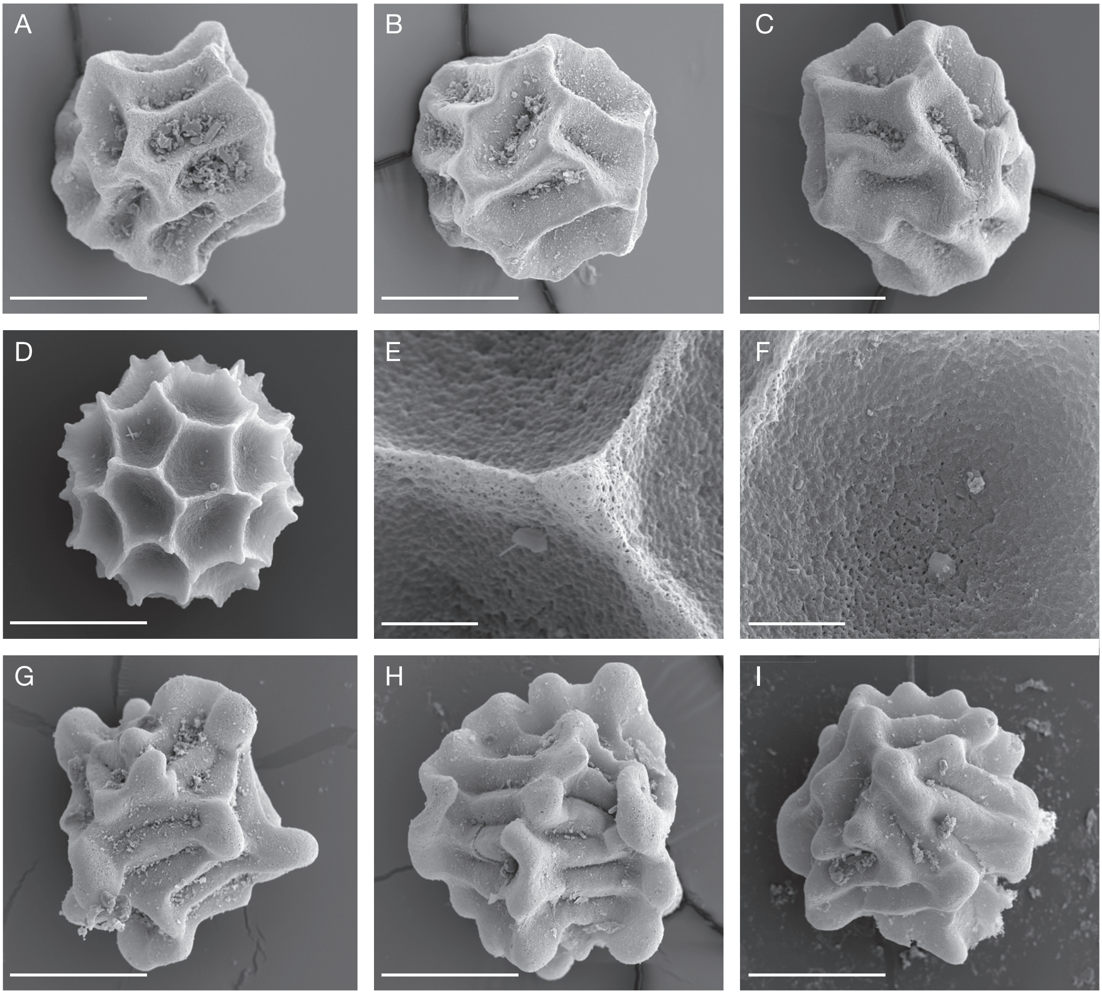

FIG. 3. — Eggs morphology: **A**-**C**, *Eulimnadia geayi* Daday de Deés, 1926, eggs from the type specimen; **D**-**F**, *Eulimnadia magdalensis* Roessler, 1990 from Cambodia; **G**-**I**, *Eulimnadia mauritiana* (Guérin, 1837), eggs from the type specimen. Scale bars: A-D, G-I, 100 µm; E, F, 10 µm.

probably in Venezuela where Geay collected numerous other aquatic organisms (see Roubaud 1906 ; Ball & Shpeley 2005). Therefore, the occurrence of this species in Colombia is not established. Our results are identical to those published by Martin (1989) from other type specimens stored in Hungarian Museum, confirming that the specimens labelled "*E. colombica*" are in fact *E. geayi*, and by Pereira & Garcia (2001) from other Venezuelan material. Daday de Deés's (1926) analysis of eggs from the type specimen seems to be partially erroneous (see Discussion) and Colombian material reported by Roessler (1995) seems to be another species.

Eulimnadia magdalensis Roessler, 1990 (Fig. 3D-F)

Eulimnadia compressa – Daday de Deés 1926: 558.

Eulimnadia magdalensis Roessler, 1990: 596, figs 1-10. — Roessler 1995: 254, figs 1c, 2c, 3c, 4a,c, 5. — Pereira & Garcia 2001: 646, figs 5, 9E.

Type locality. — Natagaima in Tolima department, Colombia (Roessler 1990).

Material examined. — **Cambodia.** "Cochinchina" "Marais d'Angkor", 1875, Harmand, >10 eggs (MNHN-Bp325); >10 eggs (MNHN-Bp328).

Range. — Present in relatively humid tropical climate in various place in Colombia (Roessler 1990, 1995), Venezuela (Pereira & Garcia 2001), Brazil (unpublished data) and following this study in Cambodia.

Egg morphology

Spherical and ornamented by large pentagonal or hexagonal depressions with a flat bottom and narrow high ridges. Ridge intersections bear a spiniform projection. Average mature egg diameter is 183.4 µm (n = 5, SD = 4.8 µm).

Remarks

This population from Cambodia was initially determinated as *E. compressa* by Daday de Deés (1926) but the eggs are identical to South American populations of *E. magdalensis* described from Colombia (Roessler 1990, 1995) and more recently found in Venezuela (Pereira & Garcia 2001). Following Sars (1896, 1900) and Daday de Deés (1926) the same egg type is also suspected for *E. dahli*, *E. similis* and *E. garreti* suggesting a possible synonymy with *E. magdalensis* but they need to be re-examined with modern procedures.

Eulimnadia mauritiana (Guérin, 1837) (Fig 3D-I; 4A-C)

Limnadia mauritiana Guérin, 1837: 5, tab. 21, figs 1-11. — Simon 1886: 456, pl. 7, fig. 2. — Brtek 1997: 57.

Eulimnadia mauritiana – Daday de Deés 1926: 535, fig.133.

Type locality. — Mauritius Island.

Material examined. — **Mauritius.** "Île de France" with no further information (first French name of Mauritius Island), Desjardins, >100 eggs (MNHN-Bp332); >100 eggs (MNHN-Bp333); >100 eggs (MNHN-Bp334).

Range. — This species is known from the type locality only.

Egg morphology

Numerous eggs are present under the carapace and in the bottom of the bottle. Twisted eggs with cluster of lobed, rounded, wide ridges, delimiting narrow furrows. Ridge intersections of different clusters bearing prominent rounded projections. The egg external wall is abundantly and homogeneously spongy (Fig. 4D, E). Average mature egg maximum length (lobe to lobe) is 221.6 µm (n = 5, SD = 19.4 µm).

Remarks

Daday de Deés (1926) description "Ova breviter fusiformes, forma structuraque membranae speciei *Limnadia lenticularis* (L.) similibus" is compatible with our results. This is the first described species in the genus *Eulimnadia*. Its egg morphology is unique to *Eulimnadia*, though *Eulimnadia astraova* Belk, 1989 eggs have some similarities but the projections are larger and conical.

Eulimnadia minuta Daday de Deés, 1926

Eulimnadia minuta Daday de Deés, 1926: 542, fig. 135.

Limnadia minuta – Brtek 1997: 57.

Type locality. — In the area of Ivindo in Gabon.

Material examined. — **Gabon.** In the area of Ivindo (part of the French Congo at the collection time), 1907, Gravot & Cottes, 2 eggs (MNHN-Bp467).

Range. — This species is known from the type locality only.

Egg morphology

Only two eggs were found in the bottom of the bottle. One is identical to those described here for *E. magdalensis* and the other is identical to those described for *E. mauritiana* and are probably due to a contamination from *E. magdalensis* and *E. mauritiana* samples.

Remark

An extensive survey would be necessary in order to find current populations of *Eulimnadia* in Gabon.

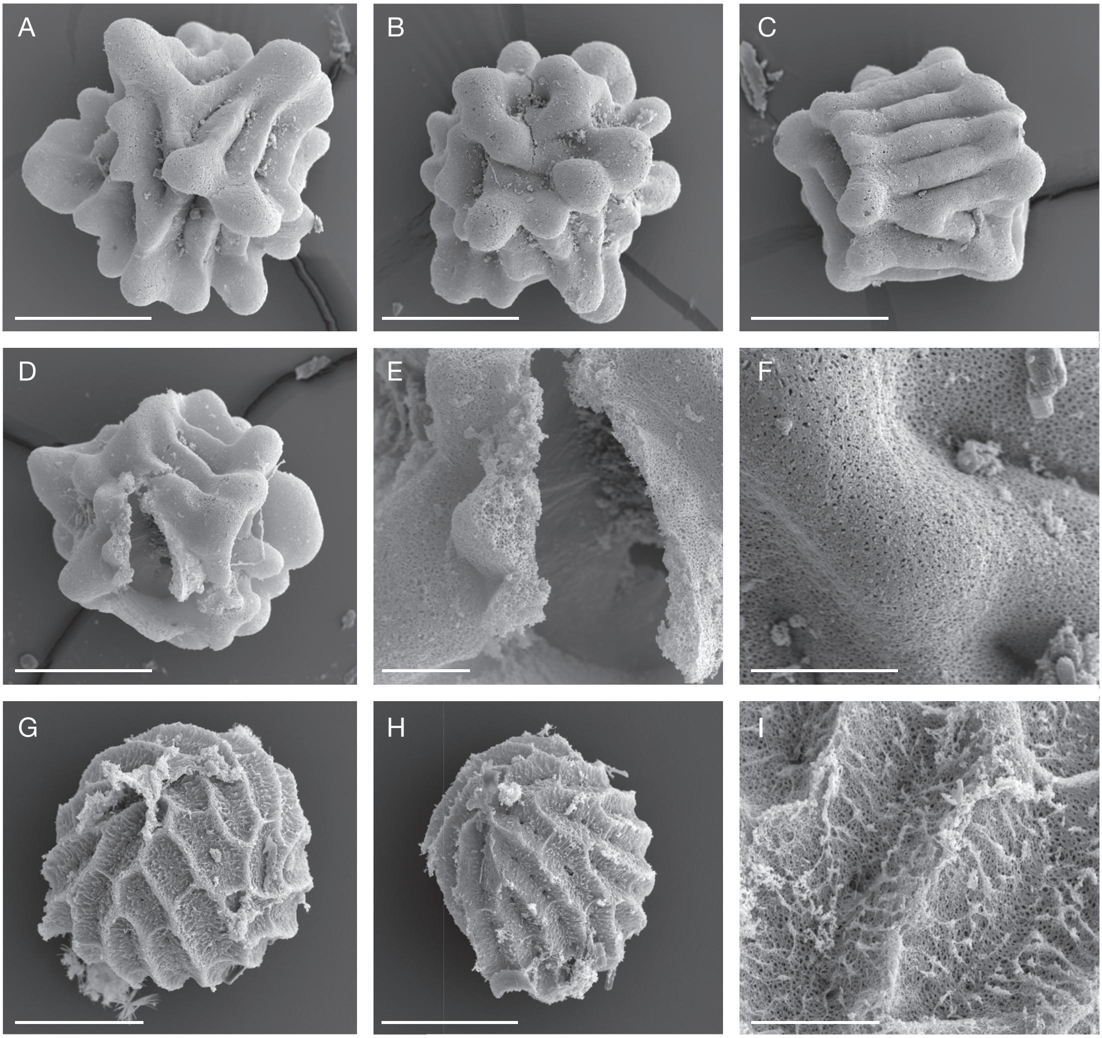

Fig. 4. — Eggs morphology: **A-F**, *Eulimnadia mauritiana* (Guérin, 1837), eggs from the type specimen; **G-I**, *Eulimnadia* sp. Scale bars: A-D, G, H, 100 µm; E, F, I, 20 µm

Eulimnadia subtropica Daday de Deés, 1926

Eulimnadia subtropica Daday de Deés, 1926: 537, fig. 134.

Limnadia subtropica – Brtek 1997: 57.

Type locality. — **Madagascar.** South, Manantantely near Fort Dauphin.

Material examined. — South of Madagascar, Manantantely near Fort Dauphin, 1901, Ch. Alluaud, female without eggs (MNHN-Bp468)

Range. — This species is known from the type locality only.

Egg morphology
No indication.

Remark
The other species known from southern Madagascar is *E. alluaudi*. An extensive survey would be necessary in order to find current populations of *Eulimnadia* near Fort Dauphin including a population of *E. subtropica* in order to describe its egg morphology.

TABLE 2. — List of *Eulimnadia* Packard, 1874 species for which the eggs were described. *****, studies not made on type specimens. **†**, description not compatible with other works made on type specimens; ° studies made under another synonym species name.

Species	Egg description without figures	Drawings or photographs after photonic observations	Egg description based on SEM	Distribution established by egg morphology	Remarks on systematics and morphology
E. acutirostris Daday de Deés, 1926	Daday de Deés 1926		this study	type locality in Niger or Mali	
E. aethiopica Daday de Deés, 1926		Daday de Deés 1926	this study	type locality in Chad or Cameroon	
E. africana (Brauer, 1877)	Brauer 1877; Daday de Deés 1926	Barnard 1929*		type locality in Sudan; probably large repartition in Africa	could be the senior synonym for other African or perhaps Asian species with spherical eggs
E. agassizi Packard, 1874	Berry 1926°		Belk 1989*; Smith 1992	USA	variability inside this species needs to be studied
E. alluaudi Daday de Deés, 1926		Daday de Deés 1926†	This study	type locality in Madagascar	South African specimens need to be compared to type specimens
E. antillarum (Baird, 1852)	Lilljeborg 1889*; Daday de Deés 1926			Santo Domingo and Mexico	no information on egg morphology from types stored in British, Hungarian and French Museums collection (Martin 1989 and this study)
E. antlei Mackin, 1940		Belk 1972*; Belk 1987*	Belk 1989*	USA	
E. astraova Belk, 1989			Belk 1989	USA	
E. belki Martin, 1989			Martin 1989	Mexico	egg similar to that of *E. colombiensis*
E. brasiliensis Sars, 1902		Sars 1902; Daday de Deés 1926	Martin 1989; Cesar 1990*†; Pereira & Garcia 2001*	Brazil and Venezuela	
E. brauerina Ishikawa, 1895		Ishikawa 1895; Daday de Deés 1926		Japon	
E. chacoensis Gurney, 1931			Martin 1989	Paraguay	partial description.
E. chaperi (Simon, 1886)			this study	India	possibly a synonym of *E. compressa*
E. colombiensis Roessler, 1989		Roessler 1989, 1990, 1995	Pereira & Garcia 2001*	Colombia and Venezuela	egg similar to that of *E. belki*
E. compressa (Baird, 1860)		Daday de Deés 1926*		India	eggs of the original type need to be investigated. The Daday de Deés's studied specimens in the MNHN are not the type specimens and represent two distinct species named here *E. chaperi* and *E. magdalensis*
E. cylindrova Belk, 1989			Belk 1989; Brendonck *et al.* 1990*; Pereira & Garcia 2001*	Mexico, Galápagos Islands and Venezuela	
E. dahli Sars, 1896	Daday de Deés 1926	Sars 1896		Australia	
E. diversa Mattox, 1937		Mattox 1937, 1939°	Belk 1989	USA	

TABLE 2. — Continuation.

Species	Egg description without figures	Drawings or photographs after photonic observations	Egg description based on SEM	Distribution established by egg morphology	Remarks on systematics and morphology
E. dubia Daday de Deés, 1926		Daday de Deés 1926		type locality in New Guinea	
E. fossimilis Pereira & Garcia, 2001			Pereira & Garcia 2001	Venezuela	
E. garretti (Richters, 1882)		Daday de Deés 1926		type locality in French Polynesia	
E. geayi Daday de Deés, 1926		Daday de Deés 1926†; Roessler 1995*†	Martin 1989; Pereira & Garcia 2001*; this study	Venezuela, Mexico	Colombian station indicated by Daday de Deés seems to be a confusion with a Venezuelan locality
E. gibba Sars, 1900	Daday de Deés 1926			type locality in India	
E. gunturensis Radhakrishna & Durga Prasad, 1976		Radhakrishna & Durga Prasad 1976		India	egg morphology needs to be reviewed
E. magdalensis Roessler, 1990		Roessler 1990, 1995	Pereira & Garcia 2001*	Colombia, Venezuela and Cambodia (this study)	the population of Cambodia needs to be compared with neotropical populations and could represent a separate species with identical egg morphology
E. margaretae Bond, 1934		Bond 1934	Thiéry 1996*	Oman and Yemen	comparison of egg morphology between Yemen an Oman population is necessary
E. marplesi Timms & McLay, 2005			Timms & McLay 2005	New Zeland	
E. mauritiana Guérin, 1837	Guérin 1837, Daday de Deés 1926		this study	type locality in Mauritius Island	
E. ovilunata Martin & Belk, 1989			Martin 1989; Martin & Belk 1989	Argentina	
E. ovisimilis Martin & Belk, 1989			Martin 1989; Martin & Belk 1989	Paraguay	egg similar to that of *E. texana*
E. packardiana Ishikawa, 1895		Kusumi 1961*		Japon	probably synonym with *E. brauerina*
E. similis Sars, 1900	Daday de Deés 1926	Sars 1900		type locality in India	possibly synonym with *E. compressa* or *E. chaperi*
E. taoluoensis Hu, 1986		Hu 1986	Shen & Huang 2008	China	egg morphology supports the distinction of this species with *E. brauerina*
E. texana Packard, 1871		Daday de Deés 1926*†	Belk 1989*; Pereira & Garcia 2001; Smith & Little 2003*†	USA, Venezuela	egg similar to that of *E. ovisimilis*
E. sp. – Margalef 1961		Margalef 1961		Venezuela	needs to be redescribed at the egg level
E. sp. – Smith & Wier 1999			Smith & Wier 1999	Mona Island	species status needs to be discussed
E. sp. – Shen & Huang 2008			Shen & Huang 2008	China	species not yet described
E. sp. – this study			this study	Madagascar	species not yet described

Eulimnadia sp.
(Fig. 4F-I)

Material examined. — **Madagascar.** Analamazaostra, Andasibe, réserve de Périnet, XI.1952, J. Arnoult, >100 eggs (MNHN-Bp667).

Egg morphology

Numerous eggs were found in natural position under the carapace and at the bottom of the bottle. Eggs are oblong with long depressions. The bottom of the depression is narrow as well as the top of the ridges. The slopes of the depression are finely ornamented much like lace. At high magnification, the surface of the egg has small pores (Fig. 4I). Average mature maximum diameter is 185 µm (n = 4, SD = 3.36 µm).

Remarks

This species was stored in the MNHN under the name *Limnadia* sp. and was associated with an undetermined specimen of *Lynceus*, probably coming from the same collection. The egg morphology of this species is so distinctive and constant that this population should be described as a new species.

DISCUSSION

Following recent literature and this study, I counted 48 species of *Eulimnadia*. Among these, 35 species have indications on egg morphology and only 24 species have valuable egg description using SEM observations. Egg morphology is probably the most important character in *Eulimnadia* systematics. Before 1989, eggs were infrequently described; for instance Daday de Deés (1926) described 16 eggs and drew nine eggs from 19 species in his monograph. However these characters were only considered and used as diagnostic after the referential works of Belk and Martin (Belk 1989; Martin 1989; Martin & Belk 1989). Moreover the first egg descriptions often suffered from technical limitations. For example pentagonal eggs of *Eulimnadia alluaudi* and *E. geayi* which clearly present a pentagonal appearance when looked at from a specific angle were described and drawn by Daday de Deés (1926) as spherical eggs.

More recently, the utilisation of SEM provided very precise and powerful informations and could be used to give morphological details in order to distinguish populations within species. In the present study, I used this tool to improve the knowledge of *Eulimnadia* egg morphology and systematics, and I confirmed that the detailed analysis of egg morphological characters gives strong diagnostic criteria.

In Table 2, I present an overview of the knowledge of egg morphology in *Eulimnadia* genus, combining bibliographical data and the results presented in this study. Geographical distributions are given only if supported by egg morphology comparison. Other geographical distributions from literature should be verified. Moreover, there are questions that need resolution, for instance a population described by Roessler (1995), erroneously determined as *Eulimnadia geayi*, possesses eggs with a spherical shape and large depressions as known for *Eulimnadia diversa*, and therefore needs to be studied in detail. Similarly, the *Eulimnadia* egg described by Cesar (1990) is probably from a new species and not *Eulimnadia brasiliensis* (the eggs of which were described by Martin [1989]).

Despite these problems, it is possible to construct a key for eggs of all Eulimnadia species, based on published descriptions. It appears clear that numerous species should be described in the future and that the eggs of old species should also be described or re-described.

Key to *Eulimnadia* Packard, 1874 eggs

1. Eggs cylindrical (one end may be inflated) (Fig. 3A) 2
— Eggs not cylindrical (Fig. 1A or Fig. 3G) 7

2. Ends flat 3
— One end domed (Fig. 2C) 5

3. Ridges extending obliquely along cylinder length .... *E. cylindrova*
— Ridges extending parallel along cylinder length 4

4. Rim inflated .... *E. colombiensis*/*E. belki*
— Rim not inflated .... *E. taoluoensis*

5. Two ends approximately with the same diameter .... *E. texana*/*E. ovisimilis*
— One end slightly wider than the other and domed (Fig. 2C) 6

6. Dome end moderately inflated, ridges narrow .... *E. geayi* (Fig. 3A)
— Dome end very inflated, ridges rounded and wide .... *E. alluaudi* (Fig. 2C)

7. Eggs spherical or oval (Fig. 1A) 8
— Eggs not spherical or oval (Fig. 3G) 20

8. Eggs oval .... *Eulimnadia* sp. this study (Fig. 4G)
— Eggs spherical (Fig. 1A) 9

9. Long grooves arranged spirally .... *E. acutirostris* (Fig. 1A)
— Other type of ornamentation (Fig. 1E or 2F) 10

10. Long and narrow depressions .... *E. fossimilis*
— Relatively short depressions (Fig. 1E or 2F). 11

11. Large depressions defined by interconnected ridges (Fig. 2F) 12
— Small depressions (Fig. 1E) 16

12. Ridge interconnections with projections (Fig. 2F) 13
— Ridge interconnections without projections 15

13. Ridge interconnections with linguiform lamellar extensions .... *E. marplesi*
— Ridge interconnections with spiniform projections (Fig. 2F) 14

14. Depression bottoms with holes or furrows .... *E. chaperi* (Fig. 2F)
— Depression bottoms smooth .... *E. magdalensis* (Fig. 3D)

15. Ridges rounded .... *E. diversa*
— Ridges acute .... *E. agassizii*

16. Depression with a central rounded dome .... *E. ovilunata*
— Depression without central dome (Fig. 1E) 17

17. Ridges acute .... *E. aethiopica* (Fig. 1E)
— Ridges rounded 18

18. Ridges ornamented .... *E. antlei*
— Ridges smooth 19

19. Depressions irregular .... *E. brasiliensis*
— Depressions narrow and relatively regular ....
.... *E. margaretae*/*E.* sp. in Yan-bin & Di-ying 2008

20. Eggs exhibiting torsion .... *E. mauritiana* (Fig. 3G)
— Eggs irregular with large conical projections .... *E. astraova*

For insufficiently known species with poorly understood egg morphology, probable affiliations to the key are given below with a list of most similar egg morphology of known species:

E. africana .... (11b) *E. ovilunata*, *E. aethiopica*, *E. antlei*, *E. brasiliensis*, *E. margaretae*
E. antillarum .... (1a) *E. cylindrova*, *E. colombiensis*, *E belki*, *E. taoluoensis*, *E. texana*, *E. ovisimilis*, *E. geayi*, *E. alluaudi*?
E. brauerina .... (7b) *E. mauritiana*, *E. astraova*
E. chaocensis .... (1a) *E. cylindrova*, *E. colombiensis*, *E. belki*, *E. taoluoensis*, *E. texana*, *E. ovisimilis*, *E. geayi*, *E. alluaudi*
E. compressa .... (13b) *E. chaperi*, *E. magdalensis*?
E. dalhi .... (13b) *E. chaperi*, *E. magdalensis*
E. dubia .... (11b) *E. ovilunata*, *E. aethiopica*, *E. antlei*, *E. brasiliensis*, *E. margaretae*
E. garreti .... (13b) *E. chaperi*, *E. magdalensis*
E. packardiana .... (7b) *E. mauritiana*, *E. astraova*
E. similis .... (13b) *E. chaperi*, *E. magdalensis*

In considering the results of this study, I have a number of concerns for the future taxonomic work on *Eulimnadia*. Firstly, the type specimens need a careful re-examination of egg morphologies: eggs need to be in sufficient quantity and if possible taken from under the carapace and in the bottom of the container where the type specimens are stored. The small size of Limnadiidae eggs and the poor manipulation of the animals during examination or transfer can result in an unacceptable risk of egg contamination. In the case of the MNHN collection the seven samples were contaminated with eggs of five species: *E. acutirostris*, *E. magdalensis*, *E. geayi*, *E. mauritiana* and *E. chaperi* (see Table 1). Only the presence of clustered eggs under the carapace is good evidence that these eggs are not from another sample. However, in collection, eggs can easily slip under the carapace and an isolated egg in contact with the animal is not evidence that the egg was originally borne by that animal. Precautions need to be taken when handling the bottom material in collection containers, in order to keep the eggs with correct animals or in an associated separate container.

Secondly, the same species from a type locality could be studied in several institutions and this comparative examination could provide a confirmation of the egg description. In the case where eggs are not available or usable in the type collections, the identification of this species in other samples could be very difficult or impossible. A solution would be to find new populations of the same species through an intensive examination in the area of the type locality (in the case where this information is known precisely enough). However in a relatively small area, the cohabitation of several *Eulimnadia* species could give an insuperable difficulty. Old citations from sites other than the type locality are problematic as adult morphological characters used in the past are probably not relevant.

Thirdly, in order to improve our understanding of the systematics of this family, it is important to describe or redescribe the egg morphology of types stored in collections. In addition, eggs from other populations need to be carefully described and compared to the type specimens. However, egg morphology also need to be associated with adult morphological characters. For example two pairs of species have virtually the same morphology: *E. texana* with *E. ovissimilis* and *E. colombiensis* with *E. belki* (Martin & Belk 1989 and Pereira & Garcia 2001). However in these cases the males have a different rostrum morphology, supporting the species distinction. Considering these results, all future species descriptions need to explain the determination method and, especially give the method of observations (SEM, stereomicroscope) of the shape of the egg.

The diversity of *Eulimnadia* eggs is important and comparable with the important morphological egg variation recently described among *Limnadopsis* (Timms 2009). Then a comprehensive comparison is necessary including other genera in order to understand the origin of this diversity. It is interesting that cylindrical eggs are found in several species of *Eulimnadia* (Belk 1989; Roessler 1989 and Shen & Huang 2008) but also in *Limnadopsis parvispinus* Henry, 1924 (Pabst & Richter 2004, Timms 2009). Similarly, torsioned eggs reported for *Eulimnadia mauritiana* (this study) are also found in *Limnadia lenticularis* (Martin 1989; Thiéry & Gasc 1991) and *L. oriquinensis* Roessler, 1991 (Roessler 1990, 1991, 1995). Spherical eggs with spiral ornamentation occur in *Eulimnadia acutirostris* (this study) and in *Imnadia yeyetta* (Thiéry & Gasc 1991). Following recent phylogenetic work (Hoeh *et al.* 2006; Schwentner *et al.* 2009) these variations are probably related to convergence.

Finally, ideally, molecular characters should be associated with egg morphology and may be useful to determine the exact status of each morphological species and to understand more precisely the egg shape evolution.

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